



**A STUDY OF THE STRUCTURE OF LINGULA
(GLOTTIDIA) PYRAMIDATA STIM. (DALL).**

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INTRODUCTION.

The investigation into the minute structure of *Lingula*, described in the following pages, was begun in the autumn of 1883, in the Biological Laboratory of the Johns Hopkins University, at the suggestion of Professor W. K. Brooks, who very kindly placed at my disposal a large collection of this genus, gathered at Beaufort, S. C., and partly also at the mouth of the Chesapeake Bay.

Unfortunately, these specimens had all been hardened in chromic acid, and, after making several series of sections, it was found, while some of them were preserved very well indeed, others proved to be quite unfit for histological work, chromic acid being, apparently, not the best hardening agent for *Lingulas*.

Comparatively little was, therefore, done until March, 1884, when I was able to procure a fresh lot of specimens, some of which were put through the chromic-acid process, others through picric acid, again others through osmic and acetic acid, and so on.

The results turned out to be very much in favor of the picric-acid process, and those specimens which were prepared in this way, and afterwards stained in picro- or borax-carmin, left nothing to be desired, so far as histological details are concerned. Hoping to supplement these histological studies by some embryological ones at the seaside, more especially with reference to the earlier stages, the later ones having already been worked out with much care and detail by W. K. Brooks, I have delayed publishing this work until now.

In order to determine the exact systematic position of this particular species of *Lingula*, I took some of the specimens to Prof.

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Wm. H. Dall, of the Smithsonian Inst., and the following account is a description of the genus in his own words:

“Glottidia pyramidata (Stm.) Dall.

“This brachiopod was originally described by Dr. Wm. Stimpson under the name of *Lingula pyramidata* (*Am. Journ. Sci. & Arts*, XXXIX, p. 444, 1860), and was obtained by him in North Carolina.¹ In 1870, while engaged in the study of the *Lingulas* in the National Collection, I discovered that some species were distinctly separated from the typical form of the genus, in being provided with raised fulcrum for the attachment of certain muscles, forming a median septum in one and two divaricating septa in the other valve. To this group I applied the name of *Glottidia*, which has been adopted. The type is a species very similar to southern specimens of *G. pyramidata*—namely, the *G. albida* of Hinds. There are three other closely related forms on the west coast of America; *G. semen* Brod., *G. audebarti* Brod. and *G. Palmeri* Dall. On the eastern shore of America, besides *G. pyramidata* there is another, *G. antillarum* Reeve, described in the *Conchologia Iconica* in November, 1859, from a single specimen, now in the the British Museum.

“It is not improbable that the latter will prove to be identical, when a sufficient number of specimens are collected for study, with *G. pyramidata*; in which case Reeve’s name has priority. All these species of *Glottidia* are probably descended from the same source or ancestral form, and no species have yet been found except in American waters, while on the other hand not a single species of the genus *Lingula*, in the strict sense, is known to occur in America, though all the *Glottidiae* were originally described as *Lingulae*. The true *Lingulas* are almost always attached to a fixed rock or stone, while *Glottidia* attaches itself, if at all, only when adult, and usually to a very small pebble or bit of shell.”

It is hoped that the present account of the structure of this peculiar species of brachiopod will not only throw new light on the structure of Brachiopods in general, but also aid in more closely defining the new genus, the creation of which we owe to Prof. W. H. Dall.

¹ It is now known to occur from the South Florida Keys to Chesapeake Bay.

The Shell of Lingula. (Figs. 1, 2, 3, 4.)

The structure of the shell of *Lingula* has, so far, been studied only by Gratiolet. This anatomist clearly pointed out the existence of calcareous and horny layers and their alternate arrangement. Gratiolet, however, seemed to be of the opinion that the outermost covering, which is found as a uniform layer over the entire surface of both valves of the shell, including the peduncle, and generally called the *periostracum*, is of exactly the same nature as are the so-called *horny layers* of which the great bulk of the substance of the shell is composed. Both are termed by him *horny*, and no distinction whatever is made between the two in his description. On a closer examination and comparison, the differences in the character of these two structures become, nevertheless, very apparent, and will, I think, be readily recognized. A brief description of the entire shell-structure may, therefore, seem desirable.

Beginning, then, with this outermost covering of the shell, the *periostracum*, or perhaps better called the *cuticle*, we find it to be a simple, homogeneous, comparatively thin layer or membrane, easily stained by picro-carmin and gold-chloride. Osmic acid gives it more or less of a bronze hue and borax-carmin leaves it entirely unstained. Over the area of the external surface of the shell proper it remains of uniform thickness throughout, but, as it passes from the posterior end of the valves on to the peduncle (over the entire extent of which it is uninterruptedly continued), it becomes markedly thicker and somewhat corrugated, to again assume much less thickness lower down towards the attached end of the peduncle. All around the entire circumference or margin of the shell of both dorsal and ventral valves the cuticle, as it were, overlaps the layers beneath it and forms a rather delicate, incurved margin of the shape of the letter "S" (see Fig. 3) on section, the lower curve of which fits into a cup-shaped impression in the mantle-margin, very near but external to the point where the bristles protrude, and with which it is in organic connection.

In almost all my preparations a certain class of peculiar, round little bodies are seen imbedded in the shell substance, sometimes aggregated in clusters, sometimes arranged in linear series, and at still other times they are irregularly scattered. It is immedi-

ately beneath the cuticle that the largest collections of these bodies are found. (See Fig. 4, *gl.*) They are best seen in sections stained with haematoxyline, by which not only the cuticle but also the horny layers of the shell substance proper are left unstained, while these corpuscles take on a violet color. They may, however, be also very readily observed in picro-earmine specimens.

Although these round little corpuscles, which are perfectly homogeneous bodies and entirely free from nuclei, are generally found aggregated beneath the cuticle, they are also often found irregularly scattered through the substance of the various horny layers forming part of the body of the shell. Shipley has described similar corpuscles in *Argiope*, and has come to the conclusion that they perform the function of carrying nutriment to the parts over which they are found distributed, believing them to be blood-corpuscles. Having studied these bodies from sections only, it is, of course, impossible to form a correct and positive opinion as to their physiological function, but from purely morphological grounds I regard them as being homologous, if not analogous, with those described as occurring within the organic septa, running vertically in the substance of the shell of the Testicardine Brachiopods.

Immediately adjacent to the cuticle and this layer of homogeneous round corpuscles, we find a rather broad layer of horny substance. (See Fig. 2, *h. l.*) The thickness of the horny layers varies greatly according to the age and the size of the animal; these layers can be beautifully stained with both picro-earmine and borax-earmine, which impart to them a very delicate pinkish hue. Osmic acid and haematoxyline give them a more or less greenish-yellow tint, while gold-chloride stains them a deep cherry brown, and in some cases an intense violet color. The horny substance exhibits sometimes a longitudinally, finely striated appearance, and these longitudinal striae are crossed by others at right angles to them, thus imparting to the whole a very fine, granular character. In most of my preparations the horny layers are homogeneous throughout, showing the above-mentioned round bodies imbedded within them. Internally to this first broad, horny layer, and closely adjoining it, we find a very thin calcareous layer of no peculiar structure and consisting

simply of coarse calcareous granules, which have remained unstained. In this manner the horny and calcareous layers alternate with each other, their number varying according to the size and age of the animal. These alternating layers may be observed equally well in longitudinal and transverse sections. Generally speaking, the horny layers decrease in thickness from without inward, while the calcareous ones slightly increase in thickness in the same direction; in no case, however, have I seen the latter attain a thickness equal to that of the horny layers. All the layers decrease in thickness, as well as in numbers, as we proceed from a point a little posterior to the centre of each valve towards its periphery, where, about the delicate, incurved margin, only a very thin film of the horny substance is left to support the thin cuticle. This thin film joins the supporting layer of the mantle-margin, while the cuticle may be followed a short distance over the epithelial layer of the same, and then gradually passes out of sight and fades away. The layer of ectodermal epithelium, which is very high at the margin of the mantle, is apparently pushed in between periostracum or cuticle and the supporting lamella.

In this manner, as will be found on all good transverse as well as longitudinal sections, all those horny layers composing the body of the valves of the shell become directly continuous with the supporting lamella of the most external layer of the mantle and that of the body-wall respectively. This circumstance quite explains the fact, already observed by Gratiolet, that it is impossible to remove the shell without tearing the external leaflet of the mantle and the body-wall, which together form the lining of both ventral and dorsal valves. Their continuity renders the conclusion almost obvious—namely, that they are identical in structure; in other words, the so-called horny layers of the valves of the shell of *Lingula* are nothing more nor less than a supporting substance. A further evidence in proof of this fact, if such was necessary, is that both stain alike and with equal intensity. In consequence thereof, it is furthermore not at all unlikely that these horny layers within the valves, from the fact of their being in direct organic connection with the supporting lamella of the mantle and body-walls, represent the homologues of the vertical septa found in the substance of the shells of Testi-

cardine Brachiopods, and certainly the peculiar, roundish bodies scattered through them speak in favor of this view.¹

The calcareous layers found between the horny layers are probably the result of a secretion on the part of the former, or that of a calcareous degeneration of the ectodermal cells of that part of the mantle and body-wall which is next to the shell.

The cuticle is probably either a changed original larval ectoderm, or has in some way been produced by it.

On the internal surface of the shells of the *Lingulas* which we have been studying there are found several ridges running in a longitudinal direction. The ventral shell possesses two of these, while the dorsal has only one. The two ridges on the internal surface of the ventral shell are so situated as to divide it longitudinally into three parts, two external areas and a middle one; the ridge on the dorsal shell runs in the median line, and, therefore, when the two valves are in juxtaposition, the latter would point about midway between the two ventral ridges. Longitudinally, they occupy about the posterior two-fifths of the whole length of each valve. The ventral ones converge in a direction toward the peduncle, into which they are, as it were, continued. It is these ridges which show the greatest number of the alternating layers which compose the shell, and to them is also attached the body-wall throughout their whole extent, the breadth of the mantle from about the anterior body-wall increasing in a direction towards the peduncle, the body-cavity decreasing in the same direction in the proportion that the ventral ridges converge.

The growth of the shell and peduncle probably proceeds from apposition to the supporting substance or connective-tissue layer of the body-wall of new layers from within, so that the external layers are the oldest and the internal layers are the youngest.

¹ Van Bemmelen describes certain round little bodies occurring in groups on the surface of the mantle which is next to the valves, defining them as round and sharply outlined little bodies, easily stained by carmine, and as not giving one the impression of regular cells. He noticed the greatest number of them aggregated around the bases of the mantle-papillae. Carpenter also saw these collections of roundish bodies in Testicardine Brachiopods, and thought that they might perhaps be the products of glandular secretion. We have also seen them in large numbers within the sinuses of the mantle.

The Body-Wall, Mantle and Peduncle of Lingula. (Figs. 2, 3, 4, 8, 10, 13, 14, 16.)

The intimate structural relationship which exists between these three organs, the direct continuity of their walls, and the free communication of the cavities which they enclose, seem to make it desirable to describe them together.

The so-called body-wall of *Lingula* is that portion of it which forms the body-cavity or visceral chamber, within which are contained the stomach, intestines, liver-lobules, genital glands and oviducts, and the various blood-lacunae.

The body-wall may, for convenience of description, be divided into several distinct parts—viz.: an anterior, a posterior, two lateral, a dorsal and a ventral. The dorsal and ventral body-walls are closely adherent to and covered by the valves of the shell, while the remaining parts are comparatively free.

The mantle is but a fold of the body-wall itself, extending from it, in a lateral and anterior direction, around the circumference, along the inner surface of the two valves up to their margins. The outer leaflet of the mantle is attached to all that portion of the inner surface of the valves which is not occupied by the body-cavity. The two mantle-leaflets enclose between them numerous spaces and channels, the most important of which are the so-called mantle-sinuses—four horn-like projections or excavations freely communicating with the body-cavity.

The peduncle may properly be looked upon as a worm-like, backward prolongation of the body-wall and its cavity. Its walls are in the main structurally identical with those of the body and mantle, and the somewhat tubular cavity which they enclose is in open communication with that of the body.

The structural constituents of all three are, first, an outer layer of ectodermal epithelium; second, a middle layer of supporting tissue, variously modified according to situation; and third, an inner layer of lining or peritoneal epithelium.

1. *Ectodermal Layer.*—This, over the greater part of its extent, consists of a single layer of very small cuboidal cells, composed of a homogeneous protoplasm with comparatively large and distinct oval nuclei, which latter stain remarkably well. This character of the ectodermal layer we find especially well preserved all over that surface of the mantle, body-wall and

peduncle which is attached to the valves of the shell, or, in the case of the latter, is covered by the thickened cuticle; it furthermore retains its typical form over the internal surface of the inner mantle-leaflet, extending from the body-wall to the mantle-margin, and also over the lateral body-walls. These cells, however, also present very marked changes in some situations. Thus, for instance, about the margin of the mantle they have become very much larger and elongated; their protoplasm is no longer homogeneous, but presents a very fine, granular appearance; their nuclei are very indistinct, and in some no nuclei whatever can be made out. (See Figs. 4 and 5.) They are oval in shape, and seem to be attached to the underlying supporting tissue by a narrow pedicel.

In specimens which were hardened in picric acid, and afterward stained in borax-carmine, many of the cells appeared enlarged, their nuclei having become very much displaced towards the limiting membrane. Scattered among them were found other cells, peculiar and coarsely granular, oblong and non-nucleated, or without any definable shape; some of them seem to protrude with one extremity from the mantle-margin, hanging loosely into the mantle-chamber; these are apparently amoeboid cells, having originated, not in the ectoderm, but more likely in the mesoderm within the mantle-sinuses. Between these different cells there seems to rise up from the supporting lamella a network of corpusculated fibres (see Fig. 4) with well-stained nuclei. These fibres, which anastomose freely with each other, form a wide-meshed network, which is probably intended to support the rather large cells of the mantle-margin. Over the tip of the latter the cells again become much shorter and narrower, their nuclei occupy a more central position and stain deeply; no granular cells occur here, but the cells are several layers deep. As they go on to form the hair-follicle, they become suddenly flattened, and do not resume their usual characteristic cuboidal form until they have reached the concave surface of the valves of the shell which they are destined to line. Over the remainder of the surface of the mantle, including the bladder-like pouches, called respiratory or branchial pouches, found at the base of the mantle-margin, the ectoderm is composed of a single layer of cuboidal, very regular cells, with slightly oval, well-stained nuclei.

It again differs somewhat from this simple arrangement over the anterior body-wall. Over the lophophore, the bases of the cirrhi, and those portions of the anterior body-wall immediately surrounding the oesophagus, especially over the situation of the central and lateral sub-oesophageal ganglia, the ectodermal covering becomes several layers deep, the cells changing from their ordinary cuboidal form into the more elongated shape; the nuclei becoming at the same time correspondingly smaller, longer and narrower. As it verges off from the anterior to the lateral body-walls, it again assumes its usual character.

We next find it undergoing a rather remarkable change over the posterior body-wall. (See Fig. 13, *p. b. w.*) This deserves a separate mention, and may briefly be described as passing from the attachment of the peduncle to the posterior end of the ventral valve, to the corresponding end of the dorsal valve, thus closing in the body-cavity posteriorly. It is perhaps best seen in longitudinal sagittal sections, taken near the median line, and so directed as to bisect the peduncle as well as the body of the creature. In such sections the posterior wall is seen to pass straight across from the base of the short mantle-margin of the dorsal valve towards the attachment of the peduncle to the ventral valve. Before approaching the latter, it forms a loop by passing straight backward in the direction of the same for a short distance, then turning upon itself and running forward again towards the attachment of the peduncle to the valve. After forming this loop, which, on cross-section (see Fig. 14), is seen to have more the appearance of a semi-circular pouch surrounding the base of the peduncle, the entire body-wall pushes its way into the peduncle, in reality goes to form part of this tubular structure or organ, receiving as it passes backward a very thick covering of cuticle. It is over this portion of the body-wall, and also to a certain extent within the peduncle, that the ectodermal layer of cells again appears in a somewhat modified form. The ordinary cuboidal cells have become distinctly ovoidal and much larger; their contents are granular, the granules consisting of larger and smaller, shining and strongly refracting globules, which do not take on the usual stain, but look yellowish and oily.

Besides these various modifications in the ectoderm, according to different locations, there are also found scattered over the

anterior body-wall and the inner leaflet of the mantle certain large, oval bodies occurring at almost regular intervals, and therefore imparting to these structures a rather studded appearance. These bodies appear usually very uniformly stained with undistinguishable nuclei, and in shape not unlike small taste-buds, with a very minute pore opening to the outside. Their significance is doubtful, and I have been unable to form a positive opinion about them, but think it not unlikely that they are glandular in character.

Immediately beneath the ectoderm we find the supporting substance. In certain situations, however, we have intervening between these two structures the central nervous system, which will be described separately. Certain calcareous plates, or the traces of them, may, very conveniently, be disposed of here. Of these calcareous plates, Van Bemmelen remarks that they are situated immediately beneath the ectodermal covering, and that after the lime has been dissolved out the outline of them remains distinctly visible, showing that each one is surrounded by a membrane, and upon this membrane we also find the cells which formed these plates. (See his Plate IX, Fig. 5.) What V. B. has found in Testicardine Brachiopods with regard to these calcareous plates, is in perfect accord with what we have seen in *Lingula*. In the latter (See Figs. 2, *vac.* and 15), these plates are more particularly found distributed over the inner leaflet of the mantle and the lateral body-walls. Here, after the lime has been dissolved out, they give rise to a more or less vacuolated layer immediately beneath the ectoderm, in which certain small, spindle-shaped, as well as larger and irregular-shaped, finely granular, nucleated cells are not uncommonly found attached to the membrane remaining behind. This condition of things is well seen in those specimens that had been hardened in picric acid.

2. *Supporting Tissue*.—Of all the elementary tissues composing the body of *Lingula*, this presents perhaps, without exception, the most varied forms. In its ordinary aspect it is a homogeneous layer of tissue either entirely structureless or presenting a very faintly, longitudinally striated appearance, staining deeply with most of the carmine agents. In this form it exists in the so-called horny layers of the valves of the shell, in both leaflets

of the mantle, the dorsal, ventral, and, to a certain extent, also in the lateral and posterior body-walls. In the anterior body-wall, however, and the deeper portions of the lateral body-walls, and also in the peduncle, changes occur which deviate considerably from the ordinary structureless, supporting lamella. Besides the great increase in the thickness which this tissue assumes throughout the anterior body-wall, more especially in those situations in which are found the central nervous system, the oesophageal blood-lacunae, and about the origin of the arms, the most striking difference in structure is in its well-defined cellular elements. (Fig. 20, *c. c.*) The cells are long and delicate, spindle-shaped, nucleated corpuscles, with rather small nuclei, which stain beautifully and deeply. The processes of these cells, usually only two in number, are comparatively broad, very finely granular or homogeneous, and scarcely at all differentiated from the surrounding tissue by staining agents. They usually traverse the entire thickness of the supporting lamella, but sometimes one of them shows two nuclear swellings instead of one, giving it a rather varicose appearance. They are remarkable for their regular arrangement and distribution.

With reference to the lateral body-walls (see Fig. 10), we find, first, a thin layer of ordinary supporting lamella adjoining the ectoderm throughout its whole extent. From this layer, rather abruptly, proceeds a reticulum consisting of supporting tissue, and extending inwardly until it has reached a considerable thickness. The nuclei seen here and there within the tissue remind one of branched connective tissue-corpuscles, the processes of which anastomose with one another to form this network. The rather large meshes of this reticulum are filled with a finely granular, jelly-like material, sperm-material and cross-sections of spermatozoa. The entire mass covers the internal surface of the supporting lamella like a semi-oval pad. We will return to this subject again in speaking of the genital apparatus. Almost the same structural conditions which prevail in the lateral body-walls, but to a much less extent, are found to obtain in the peduncle; here the fibres forming this network are very much finer and their nuclei correspondingly smaller.

The genital bands contained within the mantle-sinuses, also, are essentially like the preceding in their minute structure,

besides their being directly continuous with that portion of the lateral body-walls. The reticulum, however, is much less marked in these bands, having become reduced to a few small fibres, which only in a few instances have been found to anastomose; the greater part of it consists in spermatophores, in all stages of development.

In many places the supporting lamellae of the two mantle-leaflets join one another directly; in others, in which by their separation they have given rise to spaces, the most noticeable of which are the mantle-sinuses, fibrous partitions are seen reaching across from one leaflet to the other. The most important of these are found near the mantle-margin. From a certain point (marked *o* in Fig. 4) of the supporting substance of the outer leaflet several bundles of fibres pass on in two different directions; one set runs towards the margin of the shell, to be inserted at a point corresponding to the extreme end of the delicate, incurved margin of the shell, which here consists only of cuticle and a very thin layer of supporting tissue. This insertion is also external to the point of exit of the bristles from the mantle-margin. The other set of fibres, starting from the same point, becomes attached to the base of the hair-follicle. These two sets of fibres have hitherto been regarded as muscles, but it is evident, both from their structure as well as from their function, that they are nothing more nor less than supporting fibres intended to keep the bristles or hairs in a certain fixed position with relation to the mantle and shell of the animal. The attachment of the most anterior or ascending bundle of fibres to the shell-margin is interesting from the fact that its fibres spread out in a fan-shaped fashion at their point of insertion; in thus spreading out and intercommunicating with the corresponding ends of neighboring bundles and forming a very firm series of arches all around the entire margin of the shell, they are well calculated to keep this margin in a fixed position.

All the so-called mesenteric bands are simply bridges of this substance passing in various directions, but having for their purpose the fixation of the cavities through which they extend, at the same time serving perhaps other purposes.

3. *Peritoneal Epithelium*.—This consists of flattened polygonal cells with small, round, central nuclei; these cells are joined

together edgewise, and form a very thin and delicate membrane which lines the walls of the peri-visceral chamber, the mantle-sinuses and blood-lacunae; this membrane also covers all the viscera and mesenteric bands, and gives rise to blood-vascular spaces and channels within the body-cavity. The changes which peritoneal epithelium undergoes will be considered under the head of "genital apparatus."

The Muscular Apparatus of Lingula.

The anatomy of the muscular system of *Lingula* has been repeatedly described, with much thoroughness and care, by Vogt, Owen, Hancock, Woodward and Gratiolet. From a careful study, however, of the more minute structure of these muscles, differences have been revealed which would seem to make it in the highest degree doubtful that all those structures described as such, are in reality muscular in character. All the muscles in *Lingula* are composed of long, parallel fibres, traversing, as a general rule, their entire length, and belong to the variety of *smooth muscle-fibres*. There is no exception to this rule in *Lingula*, and even the posterior occlusor muscles show no trace of striation, as they have been found to do in some of the Testicardine Brachiopods. All those structures which have been described by Hancock as *parietal muscles*, and which Gratiolet has termed *muscles peaussiets*, to which may further be added the muscles contained within the arms and the peduncle, exhibiting an entirely different structure from ordinary smooth muscle-fibres, we have been led to regard, *not* as muscles, but rather as a *mesenchymatous supporting substance* possessing perhaps a certain amount of elasticity, but lacking the contractility proper to muscular tissue only.

The Vascular System of Lingula. (Figs. 6, 8, 11.)

Both Cuvier and Owen were of the opinion that the pallial sinuses opened directly into the organs designated by them as hearts. Vogt apparently confirmed their opinions by discovering the auricles of these supposed hearts, and also blood-vessels, emanating from the ventricles. Huxley was the first to question the correctness of these supposed facts as ascertained by Cuvier, Owen, Vogt and Hancock, and showed conclusively that there

were no blood-vessels given off from these pseudo-hearts at all, and that, instead of hearts, they were oviducts. Hancock also observed a central organ of circulation in both *Lingula anatina* and *L. affinis*, and found the same to differ but slightly from that of the articulated species.

This heart, which he only saw in a state of contraction, was situated on the posterior slope of the intestine, exactly as in *Waldheimia*. It is described as being pyriform and rather elongated, with the small end tapering gradually forward. A so-called branchio-systemic vein originates, according to Hancock, in the dorsal mesenteric membrane and communicates, through it and two lateral membranes attached to the oesophagus, with a system of lacunes which surround that tube at its origin much in the same way as in *Waldheimia*. The vein, as it goes backward, is described as passing between the divisions of the hepatic duct, and is here rather enlarged; it soon assumes the form of a distinct, isolated vein, in which condition it reaches the transverse dorsal ridge of the stomach, from which the gastro-parietal band originates, and at this point opens into the anterior extremity of the heart. The aorta is described as a single trunk leaving the under surface of the large or posterior extremity of the organ, and in this respect differing from that of the articulated species. The aorta is said to pass a considerable way down the straight portion of the intestine before dividing into two lateral stems, which pass outward, and, on reaching the ileo-parietal bands, are again subdivided in the usual way, one branch running forward, the other backward, in connection with these bands. Hancock has traced these branches very much farther, and also speaks of two arterial trunks entering the muscles. According to this author, then, we would have to look, in *Lingula*, for a closed system of blood-vessels with a central propelling organ of circulation.

Gratiolet, on the contrary, while admitting the existence of the vesicle of Huxley or the heart of Hancock, from his own researches on *Lingula*, prefers to adhere to the opinion of the older authors, and continues to look upon the oviducts as hearts, regarding the heart of Hancock as only an accessory organ of the circulation. It is to be regretted that Van Bemmelen did not express his views on the vascular system in his article. Shipley, like other more recent observers, was unable to find anything

corresponding to a central circulatory organ and the system of vessels, or the accessory pulsatile vesicles described by Hancock, in *Argiope*. The blood, he says, is contained in a number of vessels, which run irregularly within the tissues of the body, but which chiefly lie in the mantle and that part of the body-wall lining the shell. Shipley found it impossible to make out distinct walls to these vessels, which appeared to him to be mere slits in the tissues. They were found to be especially numerous at the posterior end of the ventral shell and in the angle formed by the posterior border of the triangular septum and the dorsal shell.

The blood-corpuscles, according to the description given us by Shipley, are large in comparison with the other cells of *Argiope*; stain deeply around their circumference, and possess no nuclei.

According to Schulgin, *Argiope* has no central circulating organ nor a closed system of blood-vessels, but a system of peripheral lacunae communicating with the body-cavity. The blood-corpuscles are kept in motion by the ciliated character of the lining peritoneal epithelium.

Prof. Morse seems to have proved the correctness of the latter statement by actual observation in *Lingula pyramidata*, and Brooks, in larval lingulas, has observed blood-corpuscles being constantly driven in and out of the mantle-sinuses through the irregular contractions of the body-wall. Morse compares the circulation going on within the different mesenteric bands to the pseudo-haemal system of authors, and was unable to make out the vesicle on the dorsum of the alimentary canal described by Hancock, and thought by him to be the heart.

Thus, it will be seen that the elaborate circulatory apparatus described by Hancock, in his excellent and comprehensive monograph, has not been found by any subsequent writer on *Lingula*. Neither the central organ of circulation nor the system of blood-vessels connected with it seem to exist in *Lingula*, as they were described by him.

Our own observations have been only confirmatory of the views held by Shipley, Schulgin and Morse, and the most careful search after the central propelling organ over the posterior slope of the stomach invariably proved unsuccessful in every new series of transverse sections which was made. There are, however, on both sides of the oesophagus (see Fig. 11, *lac.*) two oblong

tubular organs, generally found crowded with blood-corpuscles and extending from the peri-visceral chamber up to the origin of the arms, into the base of which they apparently empty themselves, communicating by a diverticulum with the sub-oesophageal sinuses. Since, however, they also possess a thin layer of this ubiquitous supporting tissue, they can hardly be supposed to be very contractile and in any way aid in the propulsion of the fluid which they contain. Within the mantle and throughout the anterior body-wall, blood-corpuscles are found in spaces of the supporting substance lined by a layer of peritoneal epithelium, which in my sections did not show any cilia. The accumulations of blood-corpuscles found within the visceral chamber seemed either free, or surrounded by a thin membrane which was composed of peritoneal epithelium only.

There seems to exist still a considerable degree of doubt and uncertainty as regards the true nature of certain cellular elements found floating in the circulating fluids within the body-cavity, and the various other spaces and cavities communicating with the same. In *Lingula* I was able to make out four different kinds of corpuscles floating in the circulating fluid. There is, first, a small, round, granular corpuscle (Fig. 4, *y, o*), more frequently found within the mantle-sinuses and their branches, and sometimes within the large sub-oesophageal blood-lacunae and other parts of the body-cavity. In general appearance these corpuscles do not look very unlike white blood-corpuscles; their contents are granular, their outline is sometimes round, sometimes very irregular, and a nucleus of good size may almost always be found in them; they stain well in borax-carmin, and are to all appearances endowed with amoeboid movement. Their development may easily be traced from the peritoneal epithelium lining the mantle-sinuses, and to a slight extent also from that which lines the mesenchymatous tissue of the lateral body-walls, as well as from the epithelium which covers the viscera.

From a careful study of these interesting bodies, I have been led to regard them as young ova which sooner or later become transformed into fully developed ones. In fact, their development may easily be followed in the mantle-sinuses, where all the stages from peritoneal epithelium to completely developed ova may be found. It may be possible that during the intervals of the

breeding season they remain undeveloped. Secondly, we frequently meet with peculiar, spindle-shaped, or oblong, ovoid, striated bodies already figured and described by Hancock and Gratiolet, and by the former called spermatophores, by the latter regarded as young Lingulas, and by subsequent observers mistaken for blood-corpuscles (Fig. 15, *sp.*); they are found in the same situations as the preceding, and their development from the peritoneal epithelium seems to me an obvious conclusion. The third class of corpuscles have already been described in connection with the structure of the shell; they are the smallest of them all, and are of about the size of the nucleolus in a fully developed ovum; they stain very uniformly in most staining agents, have a sharply defined, round contour, and possess no nuclei; they are found in greatest abundance beneath the cuticle of the shell, and to a less extent also within the mantle-sinuses. The fourth and last class of corpuscles, which are found in greater quantity by far than any of the preceding, are round or slightly ovoidal bodies, of a homogeneous protoplasm, with a sharply defined limiting membrane and a small, usually eccentric, nucleus. Both nucleus and limiting membrane are distinctly stained, while its other contents remain unstained. These are the blood-corpuscles proper.

The Alimentary Canal. (Figs. 6, 7, 9, 11, 12, 20.)

According to Vogt, the intestinal canal of Lingula opens to the exterior and retains about the same width throughout its whole extent. No description of the digestive system is given by either Gratiolet or Van Bemmelen. Shipley, while describing the course and attachment of the different mesenteric bands, says nothing of the histological structure of the different parts of the alimentary canal.

In Argiope, the alimentary tract is said by Schulgin to terminate blindly. The walls of the stomach are described by him as consisting of two layers—namely, an external layer of connective tissue and an internal epithelial layer. The cells of the epithelial layer are said to be narrow, high, and provided with cilia. With reference to these ciliated cells which line the intestinal canal, Schulgin says that each one of them is filled with a *granular protoplasm* which sometimes is found predominating in the upper half of the cells, sometimes in the lower half;

and he has found that when an animal is killed just after taking it out of the sea-water, the granules occupy the more centrally located portion of the cells—that is, the part nearest the lumen of the canal; and that when an animal is killed after having been kept in filtered sea-water for a few days, the granules, on the contrary, occupy the more peripheral portion of the cells. The greatest number of cilia, according to Schulgin, are found during digestion. Schulgin, no doubt, is correct so far as the granular portion of the wall of the intestinal canal is concerned during the intervals and during the act of digestion. So far, however, as the length and the number of cilia are concerned, I must, from my observations on *Lingula*, question his statement that they are most developed during digestion. In the specimens which were dredged during the month of March, I found the alimentary canal almost completely empty; only a few sparse, large, greenish cells were seen within the liver-lobules. In those specimens, however, which were collected during July and August, the entire intestinal canal, including stomach and liver-lobules, was crowded to distension with diatoms, desmids and other vegetable, and also some mineral, matter. No cilia were observed in such specimens, and the wall of the canal was thin when compared to that of some of my winter specimens. In the latter, the cilia (Figs. 9 and 12) were very long and the granular portion of the wall of the intestine seemed very rich and stained unusually deep, so that I am rather forced to believe that the cilia, during the stage of starvation of the animal, are very much longer and the intestinal canal thicker than during full digestion.

The digestive apparatus of *Lingula* may be conveniently divided into three parts—viz.: The mouth and oesophagus, the stomach and liver-lobules and the intestinal canal proper. The front portion of the alimentary canal (see Fig. 6) of *Lingula*, by which is meant the mouth and the oesophagus, forms a horn-like projection through the anterior body-wall. The mouth-opening lies flattened between the ventral valve and the sub-oesophageal blood-lacunes rising up between it and the oesophagus. The opening of the mouth as it looks towards the ventral valve is partially surrounded with a wreath of tentacles, which is, no doubt, calculated to create a current of nutrient material in that direction. From the mouth the alimentary canal pursues a slightly

forward and backward course; then, bending upon itself, it runs straight backward parallel with the long axis of the body of the animal to enter the stomach. The convexity of the canal, then, and not the mouth-opening, forms the most anterior extremity of the alimentary canal. Perhaps the most striking difference in structure between this and the remaining portions of the alimentary canal, is in the fact that the mouth and oesophagus are surrounded on all sides by two layers of strong and dense supporting tissue between which numerous blood-channels wind their way in all directions. One of these layers of supporting substance belongs to the oesophagus proper and the other underlies the general ectodermal covering; the former is continued all over the entire canal and the latter passes into the body-wall.

The largest blood-channels are found to occupy the concavity of the horn, the smallest the dorsum or convexity of the canal; between these two are the lateral ones, intermediate in size. They all communicate with the body-cavity either directly or indirectly, and like it are lined by peritoneal epithelium. Otherwise the mouth and oesophagus do not differ materially in structure from the rest of the alimentary tract. Three layers may generally be distinguished—namely, an outer layer of connective or supporting tissue, a middle layer which consists of granules or very small cells, and an inner or ciliated layer. The middle layer is by far the thickest of them all, and seems to consist of very minute cellular elements which secrete the digestive fluid. Scattered through this layer are found certain cells, shown in Fig. 6, *g. c.*, but better seen in Fig. 20, which I think are apolar ganglion-cells, and may be the remains of some larval sense-organ; the cells are found near the circum-oesophageal commissure only.

The apparent great strength of the tissues surrounding the most anterior extremity of the canal, properly designated as the mouth, and the prominences in the wall itself, seem to imply a certain power for grinding the most solid food-particles before they pass on into the oesophagus.

At a point marked *v* in Fig. 6 will be found a small bundle of supporting fibres passing between the two layers of the supporting tissue. These fibres surround the alimentary canal like a collar in this situation, and are, in transverse sections, found to

be continuous with the several bundles of fibres passing between the large blood-lacunae and the wall of the oesophagus on its ventral side. This valve-like structure may perhaps be looked upon as the dividing line between mouth and oesophagus, and also as having something to do with opening and closing, or at least with rendering the canal wider or narrower, as the case may be. Immediately behind this point the canal becomes considerably wider for a short distance, and just as it enters the body-cavity its lumen becomes very narrow.

Shortly after its entry into the body-cavity, the oesophagus joins the stomach, which is the widest portion of the entire alimentary canal. The stomach gives off several large and broad canals, which repeatedly bifurcate and at last terminate in blind pouches, the so-called liver-lobules. Inasmuch as we have found that the origin of these canals from the stomach occurs with comparatively great regularity in the several series of sections which we have examined with regard to this point, an account of it seems desirable.

The first of these canals is given off on the ventral side; it is short and broad, and divides immediately into two large lateral branches, which in their turn divide and subdivide, and finally terminate in blind pouches. Immediately behind this, the stomach, in cross-sections, presents a rather triangular shape, one of the angles pointing dorsally, the other two ventro-laterally. It is from the dorsal angle that the next canal is given off; it is broad and short, and immediately divides into two branches running at right angles to it and terminating as usual. Next behind this arises another ventral process, much narrower and longer than either of the two preceding ones and nearly reaching the ventral valve before dividing as the rest. The stomach now has assumed a more quadrangular shape in cross-sections, being compressed in a ventro-dorsal direction, convex dorsally and concave ventrally. The fourth diverticulum starts off from the left dorsal angle of the stomach and pursues a direct lateral course towards the left side, while the fifth branch runs from the right dorsal angle and is directed straight towards the right side. In all, five large branches are given off.

The structure of the walls of the stomach is like that of the oesophagus; but the liver-lobules differ very materially from the

ordinary histological structure of the alimentary canal. Fig. 7 is a section representing them, very much magnified. As may be seen, they consist of a thin, loose and supple layer of supporting tissue covered with peritoneal epithelium and often surrounded by numerous blood-corpuscles; an internal layer of well-defined round or polygonal granular cells possessing very distinctly round nuclei and nucleoli. The central lumen of these little pouches is occupied by some very faintly differentiated, round, cellular bodies with long processes of the same material, looking not unlike mucous shreds and probably consisting of secreted fluid coagulated by the reagents used in hardening these tissues and disintegrated cell-structures.

Behind the stomach the alimentary canal assumes again a more rounded form, its walls becoming thicker and appearing less folded (Fig. 9); the part extending from the stomach to the termination of the canal may be termed the intestinal canal proper.

This portion of the alimentary canal passes backward until it has reached the posterior extremity of the body-cavity, always keeping nearer the dorsal than the ventral half; it then forms either a loop or, in some cases also, it simply makes a turn in a forward direction until it reaches the ventral valve passing along its extreme right side, where the latter is joined by the lateral body-wall; it finally becomes very much narrowed, and perforates the body-wall at about the level of the junction of the anterior with the lateral portion, to open to the outside or, in other words, into the mantle-chamber. Throughout its whole length the various mesenteric bands, consisting of supporting tissue, tend to keep it in place. The opening of the anus seems to be valve-like, running for a short distance within the supporting layer of the body-wall before opening to the exterior.

The Nervous System. (Figs. 6, 17, 18, 19.)

It is a fact well recognized by zoologists that the investigation into the structure of the nervous system of the Brachiopoda is accompanied with the greatest difficulty. So far as *Lingula* is concerned, nothing is as yet known with regard to the histological structure of its nervous apparatus. So able and distinguished an investigator as Hancock confesses that he was not able to even

detect the presence of the sub-oesophageal ganglion in this creature. Owen just mentions the fact that he has seen it; and Vogt, also, I believe, must have noticed it, for he says: "The nervous system is probably situated within the sac formed by the peri-visceral wall near the gullet." The description of the nervous system given by Professor Brooks, in his studies on the development of *Lingula*, is both significant and interesting in this connection. In certain of the early stages, Brooks describes and figures (see his Figs. 3, 5 and 6) the nervous system as consisting of a commissural ring which encircles the oesophagus at its union with the stomach, carrying one ventral ganglionic enlargement, two lateral ganglia and two dorsal otcysts.

The nervous system of other Brachiopods, however, is much better known than that of *Lingula*, and Hancock has given us a very complete and detailed account of its anatomy in several Testicardine Brachiopods, especially *Waldheimia australis*. His conclusions were that the nervous collar is situated mainly at the commencement of the alimentary tube, and that with this collar are connected five nervous ganglia, three of which, on account of their superior size, might be assumed to be the principal ganglia.

These nerve-centres, he says, lie amid blood-lacunae, between the two membranes, forming the anterior wall of the peri-visceral cavity immediately below the oesophagus, or rather behind it, on account of the mouth being bent down. He distinctly states that the largest is anterior, the other two form a pair and are lateral and elongated transversely across the median line, and describes the ganglion as having the anterior and posterior margins parallel and the sides sloping inward and backward; it is said to be prolonged into a stout nerve in front, which immediately divides into an upper and a lower trunk.

This description by Hancock of the anatomy of the nervous system in the Brachiopoda has recently been criticised by Van Bemmelen. It is for the sake of comparison that these views have been cited at some length, and for the same reason we will quote those of Van Bemmelen.

Van Bemmelen was perhaps the first to investigate the structure of the Brachiopoda according to modern methods, and the account which he has given us, accompanied as it is with a

number of very finely executed plates, is the most complete of any we possess at present. The descriptions of the anatomy and disposition of the more noticeable ganglia by the two authors vary somewhat.

Hancock, on the one hand, finds five nervous ganglia connected with the nerve-collar; Van Bemmelen, on the other hand, describes them as only two, an inferior and a superior. The lateral ganglia of H. are, according to V. B., only parts of the more centrally situated large sub-oesophageal ganglion with which they were found to be fused, and hence could not be regarded as separate. V. B. further speaks of one superior or supra-oesophageal ganglion situated in the middle line, while H. describes two ganglia in this situation, situated on either side of, but near, the median line. The views of V. B. with regard to the disposition of the different nervous ganglia are, as he says himself, based mainly upon a study of transverse sections.

Shipleigh describes a sub-oesophageal ganglion situated in the epidermis of that part of the body-wall which is immediately posterior to the base of the tentacles which overhang the mouth, just where the body-wall turns to form the mantle of the ventral shell, as consisting of two parts—namely, an anterior, which is a well-marked elevation formed by a ridge of the homogeneous supporting substance, covered by a layer of nervous cells and fibres, and a posterior portion, which is simply a narrow band of nervous tissue not very conspicuous. The supra-oesophageal ganglion is described by Shipleigh as elongated, and lying in the ectoderm just anterior to the base of the lip which overshadows the mouth; this ganglion is said to be very small in comparison with the sub-oesophageal.

Finally, Schulgin, studying the nervous system from sections as well as teased preparations, locates the sub-oesophageal ganglion deep under the mouth, at a point where the ileo-parietal joins the ventral band beneath the lower margin of the disc of tentacles. Behind (dorsally ?) he finds two small lateral ganglions, directly connected with the lower ganglion by fine nerve-fibres. The dorsal connection between these two he was unable to trace, but suspects that they are so connected as to complete the circum-oesophageal nerve-ring, on account of

their sending off fine nerve-fibres which tend to meet in the middle line. Schulgin then speaks of a sense-organ, which he locates in the anterior body-wall, just where the great sub-oesophageal ganglion of authors is usually situated.

From this brief review of the accounts of the nervous system, we may readily see that discrepancies still exist. On closer examination, however, they will be found unimportant. Nevertheless, from our own investigation into the nervous system of *Lingula*, we have been led to adhere to the number and division of the nervous ganglia originally put forth by Hancock for *Waldheimia australis*. There are in *Lingula* five distinct nervous ganglia connected with the circum-oesophageal commissure. These are sufficiently separate and distinct from each other so as to justify their being accepted as different and as needing separate description. The number of the ganglia in *Lingula*, therefore, agrees with that found in *Waldheimia* by Hancock. These five ganglia may, from their respective situations in this instance, be described as the *great central sub-oesophageal*, the two *ventro-lateral*, and the two *dorso-lateral* or *supra-oesophageal* ganglia. The first-named is also the largest; the second comes next in size, and the third is the smallest of them all. All the ganglia are enclosed between a layer of ectodermal epithelium, forming their outer covering, and consisting of one or more layers of cells, and a layer of supporting substance, of varying thickness, forming the floor.

The great central sub-oesophageal ganglion occupies the entire extent of that portion of the anterior body-wall which is situated between the oesophageal blood-lacunes and the mantle lining the ventral valve. In shape it is plano-convex, the convexity being anteriorly. At the dorso-lateral angle on either side, the ganglion is connected by a thick commissure with the two ventro-lateral ganglia. As may be seen, this account regarding the extent and location of this ganglion agrees perfectly with that given by all the authors above quoted, with the exception of one. Schulgin describes a condition of things as existing in *Argiope Kowalewskii* which is somewhat remarkable, if not unique. In about the situation where the sub-oesophageal ganglion is found in all the other Testicardine Brachiopods, as well as in *Lingula*, he locates two sense-organs. (See his Figs. 17 and 18.) On page 137 of

his article he says: "Argiope possesses not far from the mouth a very characteristic accumulation of cells upon the integument, which plays the part of a sense-organ. This organ consists of two parallel, longitudinal heaps of cells, one of which, nearest the mouth, containing specific, and the other, farthest away from the mouth, containing epithelial, cells." The former is spoken of as being in direct connection with the central or sub-oesophageal ganglion, and as not being an organ of sight on account of the absence of pigment. The central oesophageal ganglion—which, therefore, must be very small—he locates much nearer the oesophagus and the tentacular disc than is ordinarily the case in other instances. No such sense-organ as Schulgin describes in *Argiope* exists in the *Lingulas* we have been studying.

The next ganglia, those which we have designated as *ventro-lateral*, are two in number. They are situated close by the sides of the great oesophageal blood-lacunes, the outer boundaries of which they cover to a certain extent, being, of course, separated from them by a thick layer of a homogeneous supporting substance. Their situation with relation to the oesophagus is ventral, and to the great oesophageal ganglion it is dorso-lateral. Their shape may be said to be semi-oval, the convexity pointing to the right and left sides respectively, and the plain surface towards the lacunes. Both ganglia are connected with each other by a strong transverse commissure running straight across from side to side on the ventral aspect of the lacunes, or on the dorsal side of the great sub-oesophageal ganglion—that is, between the two; their outer ventral extremity is joined to the central sub-oesophageal ganglion at its dorso-lateral angle; their dorsal extremities give off the dorsal pallial nerves and afterward form the continuation of the commissure. The commissure passes on towards the posterior aspect of the roots of the arms, and here it divides into two bands, one of which passes around the oesophagus on the ventral aspect of the arm-roots, and the other over the dorsal aspect of them; from both these bands numerous fine fibres are given off to the surrounding tissues; they finally join and fuse with the supra-oesophageal ganglia.

The *supra-oesophageal* ganglia are two in number; they are

situated over the anterior aspect of the roots of the arms, extending to the sides of the most anterior and curved extremity of the alimentary tube, over which a commissure passes connecting the two. The somewhat triangular space in this situation is thus completely filled out. The nerves which these ganglia give off to the arms, and which pass off from them in a lateral direction, are exceedingly rich and unusually large and capable of being traced for some distance.

With reference to the minute histological structure of the nervous system in *Lingula*, a general uniformity obtains. The nerve and ganglion-cells, as indeed most of the other cells in this creature, are all very small, and high powers of the microscope are, therefore, to be employed, in order to see and recognize them. A good No. 9 Hartnack obj. with a No. 3 eye-piece is usually sufficient for the purpose. With such powers, the structure of the nervous system will be best revealed in specimens carefully preserved with picric acid and stained in borax-carmin. In such specimens the larger ganglia are found to consist of multipolar ganglion-cells, with broad and long processes anastomosing with each other, and forming a thick and dense network. These cells vary very much in size and shape, and possess usually round, well-stained nuclei and nucleoli; their contents are finely granular, but not uniformly so; sometimes one portion of a cell seems granular, the other portion homogeneous, and so on. Every large ganglion-cell usually gives off one long process, which passes towards the supporting lamella, and there is lost in the general felty network of the numerous fibres congregating in that situation. These processes are best seen in dorso-ventral longitudinal sections through the great sub-oesophageal ganglion (Fig. 17), and are much less noticeable in the other ganglia.

So far as the course and distribution of the different nerves are concerned, they have been so accurately described by V. B. that there remains nothing new for us to add in respect to them. We may, however, say that in all essential points the distribution and course of the various nerve-trunks in *Lingula* agree perfectly with the description given us by V. B. of Testicardine Brachiopods.

Before leaving the nervous system, mention must be made of certain cells the nature of which seems to be as yet doubtful.

In Figs. 19 and 20 will be found certain well-defined cells, strongly granular, with distinct nuclei and nucleoli, imbedded in the wall of that portion of the oesophagus which is surrounded by the nerve-ring and the ganglia in connection with it, which cells may perhaps be regarded with a certain show of reason as apolar ganglion-cells; it is also not quite improbable that they are the remains of some larval sense-organ, rather than salivary corpuscles.

Schulgin also mentions certain sensory cells which he found between ectoderm cells in some situations. I have not been able to convince myself with any degree of certainty of their existence, unless some of the peculiar inter- or sub-ectodermal cells shown in Figs. 2, 4 and 5, are sensory in nature, which might possibly be the case.

The Generative Organs. (Figs. 4, 10, 15 and 16.)

The description of the genital apparatus of *Lingula* may be divided into two parts—namely: 1. That of the *genital glands*, which are the organs producing the ova and spermatozoa respectively; and 2. That of the *oviducts* or *segmental organs* (Morse), which conduct the spermatozoa and ova into the pallial chamber and thence into the sea-water.

The segmental organs have received by far the greatest amount of attention from the investigators of this class of animals, while the genital glands, more especially those which produce the spermatozoa, are as yet but very imperfectly understood; and one of the main objects of this paper is to throw some additional light on this subject, if possible.

Before proceeding to a more minute description of the genital organs as they exist in the creature we have been studying, it will be necessary to take a look over the somewhat extensive literature of this field of research, in order to realize the present state of our knowledge.

Cuvier, Owen and Vogt, the oldest writers on Brachiopods, as has been mentioned before, had no hesitation whatever in pronouncing as hearts what we now know to be oviducts, or perhaps what we might more correctly term, with Morse, segmental organs; and even Gratiolet, who wrote some time after Hancock

had published his views on the subject, still continued to adhere to the opinions of these older writers.

It is more especially Hancock's comprehensive article on the anatomy of Brachiopods which claims our attention for a moment. The views expressed by him very justly became the most generally accepted ones of his day, and it is perhaps but fair to state, in general terms, that even at the present day most of his views, advanced nearly thirty years ago, cannot be overthrown.

Of the genitalia of *Waldheimia australis*, Hancock says that they are formed of thick bands somewhat convoluted and branched; that they are of a yellow color and are thrust into the trunks and main branches of the great pallial sinuses. There are four of these bands, two in each lobe; those on the dorsal lobe are single and occupy the two outer or lateral sinuses, extending from behind the oclclisor muscles to within a short distance of the anterior margin of the mantle.

Their posterior extremities reach the peri-visceral chamber. The ventral pair extend as far forward as the dorsal, and are double—that is, each forms a loop the free extremities of which pass into the outer and inner sinuses of the same side; the looped portions lie within the peri-visceral chamber at the sides below the oviducts.

These genital bands, according to Hancock, are attached to the inner lamina of the mantle throughout their whole extent by a membrane which, originating in the lamina, passes into a groove extending along the under surface of this genital band. The genital or pallial artery is said to run along the edge of this membrane, and has the reproductive organs developed around it. On closer inspection he finds that these organs are in reality developed between the two membranes which, it will be afterwards seen, compose the inner lamina of the mantle, and bulging out the interior of these, become suspended, as it were, in the pallial sinuses.

Somewhat farther on in the text, Hancock says that the genitalia are very perceptibly composed of two elements—the yellow, ovigerous substance which forms the chief mass, and a red material, for the most part distributed over the surface of this organ. When, he remarks, the organ is in a low state of development, this red matter forms a narrow, irregular cord, which runs

along the side of the band and is occasionally spread over the surface of it in spots and blotches. When the ova are fully developed, this substance may still be seen as small specks on the surface and throughout the mass.

This red matter, Hancock states, may prove to be the testis, and is made up of large, irregular cells inclining to oval, variable in size, and without any apparent nucleus.

This whole account refers mainly to *Waldheimia australis*.

This description of the generative glands in *Waldheimia australis*, a Testicardine Brachiopod given by Hancock, is in almost perfect accord with what we have found with regard to the genital glands in the Ecardine Brachiopod *Lingula*. Indeed, with one exception, they are identical. This exception is, that in the species of *Lingula* we have been studying, the genital bands contained within the mantle-sinuses are attached to the outer leaflet and have no genital artery, instead of their being attached to the inner leaflet of the mantle and provided with a genital artery, as is the case in *Waldheimia*.

Nevertheless, Hancock states from *Lingula*, of which he studied two species—namely, *L. anatina* and *L. affinis*—that *the reproductive organs are withdrawn altogether from the mantle-sinuses and are placed in the visceral chamber*, as they are also stated to be in *Discina*. Hancock describes the reproductive organs of *Lingula* as being very bulky, and as occupying a very large portion of the visceral chamber; they lie, he says, for the most part, behind the liver and surround the alimentary tube, forming four irregularly branched and lobed masses, two above and two below the tube, which he designates as the dorsal and ventral lobes respectively. The ovaries themselves are, according to Hancock, suspended by the parietal bands and their reflected portions, which agrees perfectly with the condition of things as they exist in *Lingula pyramidata*, so far, of course, as that portion of the generative glands is concerned which is contained within the visceral chamber.

It becomes now necessary to examine Hancock's views as to a certain reddish-yellow mass or substance which he found covering the surface of the ovaries, and which he supposed to be the testis. This substance, he remarks, assumes the form of a dendritic or branched organ as it spreads over the surface of the ovarian masses.

Over the dorsal ovaries he describes this organ as passing from behind forward in two lateral divisions, on the ventral ones in three, two lateral and one median.

He also observed, when attempting to remove the membrane forming the dorsal and ventral walls of the visceral chamber, that those dendritic organs came away with it. He was *originally* induced to believe that they were organically connected with it, but further experience, he says, convinced him of the fact that they were really a portion of the genital mass—that is, of the ovarian masses contained within the peri-visceral chamber—and had nothing to do with the body-walls. Their adhering to and coming away with these walls, he thought was explained by the pressure which was exerted on these masses by the closure of the valves.

Nevertheless, if Hancock had adhered to his original impression, and had followed it up more carefully than he did, it would, in our opinion, have led him to the true origin of these dendritic masses, which, as we will learn later on, are really organically connected with the body-walls.

That this so-called dendritic or branched organ of which Hancock speaks, was really the testicular mass, may be inferred with certainty from his own microscopical examination, which proved it to be composed of irregular cells, somewhat elliptical in form, and closely resembling the reddish substance observed in connection with the ovaries of *Waldheimia*. The cells in *Lingula*, however, appeared to him to present different stages of development, varying much in size and shape and being filled with numerous hair-like bodies resembling spermatozoa. A glance at Fig. 16, *sp.*, will, perhaps, answer the description of the bodies he describes.

Whether or no Hancock discovered the true origin of these bodies, it is sufficient for our present purposes to know that he came nearer to it than any of his successors, and that he did recognize in them their true nature, which is that they formed the male element of generation. His conclusion, therefore, that the sexes in all the Brachiopods were united, was, of course, natural enough.

Fig. 10 is a small part of a transverse section through the lateral body-wall, showing the origin and true seat of develop-

ment of the spermatophores and the epithelium covering them on their internal surfaces. All over the internal surfaces of both lateral body-walls the spermatophores are densely crowded together, forming a very thick layer, which extends far into the peri-visceral chamber, coming into close contact with the mesenteric bandlets from which the ova are principally developed, and which, therefore, the spermatophores seem to cover. Figs. 15. and 16 show their development from the genital ridges which are contained within the mantle-sinuses and their branches.

The intimate structure of the genital ridges, their loops, which hang in the peri-visceral chamber, and that of the lateral, and, to a certain extent, also of the dorsal and ventral body-walls, is in the main identical. These structures are all in direct continuity with each other, and their structural differences, which are slight, will again engage our attention at the end of this chapter.

Very different from the views of Hancock are those advanced by Gratiolet, who believes that the peculiar bodies described and named by Hancock *spermatophores*, are not spermatophores, but *young Lingulas*. Gratiolet believes *Lingula* to be an hermaphrodite animal, in which, however, hermaphroditism is not simultaneous, but rather successive; that is to say, the animal is first a male, filling the visceral cavity with a spermatie fecundating fluid to fructify the ova, which are to be developed subsequently, somewhat after the fashion of Davaine's theory of the fructification of the oyster. The structures which develop the ova also develop the spermatophores, according to Gratiolet.

Shipley, in his article on *Argiope*, makes the following remark with regard to the sexual apparatus—viz.: "Although I have not been able to find a male *Argiope*, yet I have no doubt that this genus, like the other members of its class, is dioecious. In those *Argiopes* which I have examined I find no trace of a testis, and in the allied genera, Lacaze-Duthiers describes a male generative gland in a position similar to that occupied by the ovary in *Argiope*, and I have myself seen the testis of *Megerlea* in the same position."

Strangely enough, Schulgin, one of the latest investigators of *Brachiopods*, likewise states that in all the species of *Argiope* examined by him (which include a large number) he was unable to find a single male specimen, but, nevertheless, expresses himself as very decidedly in favor of the bisexuality of *Argiope*.

The question might be asked, Could both Shipley and Schulgin perhaps have overlooked the existence of spermatophores, and misinterpreted the structures from which they are developed?

With reference to this point, Prof. Morse says that he believes that in all the Brachiopoda the sexes will be found separate, and that in *Lingula* the spermaries occur in the peri-visceral cavity in masses like the ovaries. Having studied them alive, Morse continues, it was found that while in some individuals the ovarian masses nearly filled the peri-visceral cavity, in others the spermaries occupied similar positions. According to Morse, *Lingula* and *Discina* are identical in this respect.

Van Bemmelen also believes in the sexes being separate, at least in Testicardine Brachiopods, while Oscar Schmidt holds that they are united in the same individual. It is clear, then, that the weight of evidence is in favor of the bisexuality of the group, and all the more modern authors are almost unanimous on this point. It was, therefore, only after considerable hesitation that I was forced, by the evidence before me, to believe in the fact that, so far at least as *Lingula* is concerned, the sexes are united within the same individual.

No specialized male organs of generation have so far been described as occurring in *Lingula*; but it was thought that wherever, in the female, ova were developed, in the male, spermatozoa were found to develop; and even Hancock was of that opinion, although he saw both develop side by side within the same individual.

Hancock's views are still correct, so far as the genital ridges within the mantle-sinuses are concerned. Within these, according to our interpretation, both ova and spermatophores develop side by side; it is, however, different within the peri-visceral chamber. Here the ova are confined principally to the mesenteric bands and their reflected portions—in other words, occupy a more central position with relation to the animal—while the spermatophores occupy the peripheral walls of the visceral chamber—in fact, are almost exclusively developed from the peritoneal epithelium covering (in many layers and much modified) the lateral body-walls and to a slight extent also the dorsal and ventral.

While, then, in our opinion, *Lingula* is an hermaphrodite

animal, it is nevertheless rare to find both ova and spermatozoa present in equal proportions and equally developed within the same individual. In those individuals in which, for instance, the male elements largely preponderate, fully developed ova are sometimes very few, and may even be found entirely confined to the mantle-sinuses, so that, on a superficial examination, they might be entirely overlooked. A more careful examination of an entire series of sections, however, will invariably result in finding both male and female organs of generation within the same individual.

As already mentioned, the principal seat of development of the spermatophores is the lateral body-wall. This arrangement seems to be in perfect harmony with the close apposition in some individuals of the cup-shaped internal extremity of the segmental organs to the lateral body-walls, which, so far, has remained unexplained. One of Gratiolet's objections to the view that these organs are oviducts instead of hearts, was this very circumstance. He said if they are oviducts, intended to carry the ova from the peri-visceral chamber to the exterior, their internal openings ought to be directed towards the eggstocks; meanwhile, they are closely applied to the lateral body-walls. But we know also that the internal openings of the segmental organs are not always in this position, but occupy places which would materially favor the passage of ova into them. We would, therefore, consider them as movable organs intended to take up spermatozoa or ova and carry them into the mantle-chamber at certain intervals; and in accordance with this double function the relative position of their internal openings changes: at one time it will be found snugly applied to the lateral body-walls, and then spermatophores may be seen within the oviducts; at another, their ciliated inner extremity will point directly backward towards the most posterior portion of the visceral chamber, into which fully developed ova usually drop, and under these circumstances ova may be detected within the oviducts. Having never seen either ova or spermatophores within the same oviduct, it is not to be supposed that fructification takes place inside of the animal, but rather that this occurs in the mantle-chamber or in the sea-water.

With reference to the mode of development of the ova—so far, of course, as this may be studied from sections only—it appears

to be about as follows: To begin with, we think there can now hardly be any doubt as to the ova springing directly from the cells composing the peritoneal lining membrane. The cells composing this structure are, under normal conditions, small, round or polygonal cells joined together edge to edge; they possess a well-defined and usually round nucleus, which lies imbedded within the homogeneous cell-substance. Over the mesenteric bands and their reflected portions, where ova are developed, these cells at first become roundish, lose their transparency and take on a granular character. The nucleus now seems somewhat obscured, but as development proceeds it reappears, and is now much larger than it was before. During the intervals of the breeding season the ova in this stage of development may become detached and wander about, growing larger, however, all the time, so that ova in almost all stages of development may be found floating around everywhere. Finally, the granular contents become differentiated into the yolk and the germinal vesicle is formed from the nucleus, and so is also the germinal spot. During the breeding season almost all these different stages may be studied on one single branch of mesenteric filament, the ripest ova being always found near its end and farthest away from the main stem.

The development of the spermatophores, which also takes place from peritoneal epithelium, is somewhat different. Here the nucleus seems to be the all-important element. This at first becomes slightly oval and elongated, being surrounded by a zone of clear, transparent, structureless protoplasm. The nucleus now assumes a very finely longitudinal, striated appearance, grows rapidly, until it finally entirely fills its surrounding envelope, which it seems to burst open, when it becomes a fully developed spermatophore. Fig. 16 will illustrate these points. The development of the ova is, perhaps, best followed by examining Fig. 21.

The oviducts having been repeatedly and very accurately pictured and described by most authors on the anatomy and structure of Brachiopods, it would seem superfluous to say anything more about them here, since my studies have only confirmed the correctness of the descriptions given us by the more modern authors on the subject.

REFERENCES.

R. OWEN. On the Anatomy of the Brachiopoda. Transactions of the Zool. Society of London, Vol. I, 1835.

T. H. HUXLEY. Contributions to the Anatomy of the Brachiopoda. Proceedings of the Royal Society of London, Vol. VII, 1854.

A. HANCOCK. On the Organization of the Brachiopoda. Philosophical Transactions, Vol. CXLVIII, part II.

M. PIERRE GRATIOLET. Recherches pour servir à l'histoire des Brachiopodes; première et deuxième monographies; Journal de Conchyliologie 8. 1860, 2^{me} serie IV.

EDWARD S. MORSE. On the Systematic Position of the Brachiopoda. Proceedings of the Boston Society of Natural History, Vol. XV, March 19, 1873.

EDWARD S. MORSE. On the Early Stages of Terebratulina Septentrionalis. Memoirs of the Boston Society of Natural History, Vol. II.

W. K. BROOKS. Development of Lingula. Chesapeake Zool. Laboratory. Scientific Results of the Session of 1878.

DR. I. F. VAN BEMMELEN. Untersuchungen über den anatomischen und histologischen Bau der Brachiopoda Testicardinia. Zeitschrift für Naturwissenschaft XVI. N. F. IX, 1. u. 2, Jena, Verlag von Gustav Fischer, 1883.

E. SHIPLEY. On the Development and Structure of Argiope. Mittheilungen aus der Zoologischen Station zu Neapel, IV Band, 4 Heft.

M. A. SCHULGIN. Argiope Kowalewskii. Ein Beitrag zur Kenntniss der Brachiopoden. Zeitschrift für wissenschaftliche Zoologie, Band 41. Heft I, Nov. 4, 1884, page 116.

DR. CARL VOGT. Anatomie der Lingula anatina. Neue Denkschriften der Allgem. Schweizerischen Gesellschaft für die gesammten Naturwissenschaften.

EXPLANATION OF PLATES.

PLATE XIV.

FIG. 1.—Represents a transverse section of shell and mantle from a point about midway between margin of mantle and anterior body-wall; *h. l.*, horny layer; *c. l.*, calcareous layer of shell with *cu.*, cuticle; notice the peculiar round, little globules beneath the cuticle; *ec.*, ectodermal epithelium; *m. s.*, mantle-sinus lined with *p. c.*, peritoneal epithelium; *g. r.*, generative ridge, × piece of shell and cuticle broken off. Magnif. Ocul. iii, Objective vi.

FIG. 2.—Transverse section through mantle and shell, on larger scale than preceding; letters same as in Fig. 1, showing peculiar so-called calcareous corpuscles, *c. c.*, and the vacuoles left between ectoderm and supporting lamella after treatment with picric acid, *vac.* Magn. Oc. iii, Obj. 9, Hart.

FIG. 3.—Section through margin of shell and mantle; *sh.*, shell, *cu.*, cuticle; *ec.*, ectodermal layer next to shell; *h.*, hair; *t.*, tip of margin of mantle. Magn. Oc. iii, Obj. 9.

FIG. 4.—Transverse section through margin of mantle, shell and mantle-sinus; *cu.*, cuticle; *h.*, hair; *sh.*, body of shell diagrammatically represented; *s. f.*, supporting fibres; *ec.*, ectodermal layer lining shell; *y. o.*, young ova; *g. r.*, generative ridge contained within *m. s.*, mantle-sinus; *sp.*, spermatophores; *m. m.*, mantle-margin; *ec.*, ectodermal layer; peritoneal epithelium lining the entire mantle-sinus, except over generative ridge, where it is much modified; *pl.*, plexus of corpusculated supporting fibres or sensory cells of Schulgin.

FIG. 5.—Section through part of mantle-margin; gold preparation; *s. t.*, supporting tissue and hair diagrammatically represented; mantle-margin showing large granular cells, *gr. c.*, stained a very dark, brownish-red; *f. gr. c.*, finely granular cells almost unstained; *?*, peculiar, spindle-shaped, elongated cells which may be either supporting fibres or perhaps also the sensory cells of Schulgin, to which they seem to correspond both in situation and appearance. Magn. Oc. iii, Obj. 9.

FIG. 6.—Dorso-ventral longitudinal section from borax-carminé specimen; *lac.*, space hollowed out of the supporting tissue, various sizes and all lined by peritoneal epithelium; *v.*, bundle of supporting fibres forming a sort of partition and extending laterally and horizontally to a considerable distance around that portion of the oesophagus, probably serving as a valve of some kind; *oe.*, wall of oesophagus; *cav.*, cavity of oesophagus; *cil.*, ciliated portion of oesophagus; *l. l.*, liver-lobule; *n. s.*, section of part of central sub-oesophageal ganglion; *bl.*, blood-corpuscles; *t.*, section of one of the tentacles projecting from the lower lip, *l. p.*; *s. t.*, bundles of supporting fibres running between two layers of supporting tissue, and probably subserving the same function as *v.*; *u. l.*, upper lip; *g. c.*, peculiar large cells, probably apolar ganglion-cells. Magn. Oc. iv, Obj. 6.

PLATE XV.

FIG. 7.—Section of liver-lobule, showing thin outer coat of loose supporting tissue, *st.*, with peritoneal epithelium, *p. e.*; one or two layers of large, round or polygonal granular cells next to supporting

layer, *l. g. c.*, and very large and finely granular cells, *m. c.*, in the centre, with processes looking like mucous shreds. Magn. Oc. iii, Obj. 9.

FIG. 8.—Dextro-sinistral longitudinal section of mantle intended to show the structure of the papillae, which are filled with blood-corpuscles. Magn. Oc. iii, Obj. 6.

FIG. 9.—Transverse section of intestine below stomach, showing an outer coat of loose connective or supporting tissue, in which numerous blood-corpuscles are generally found, not represented in the drawing; *w.*, wall; *cil.*, ciliated internal layer. Magn. Oc. iii, Obj. 6.

FIG. 10.—Transverse section through lateral body-wall; *ec.*, ectodermal covering; *vac.*, vacuoles; *l. c.*, lime-cells; *s. l.*, supporting lamella; *p. e.*, modified peritoneal epithelium; *r. sp.*, cross-sections of ripe spermatophores; *sp.*, spermatophores. Magn. Oc. iii, Obj. 9.

FIG. 11.—Transverse section of oesophagus, intended to show the two lateral blood-channels, *lac.*, extending between the roots of the arms and the peri-visceral chamber, and also communicating with the sub-oesophageal blood-lacunae; they are always filled with blood-corpuscles; *s. f.*, strong bands of supporting lamella separating the ventral blood-lacunae; *oe.*, oesophagus. Magn. Oc. iii, Obj. 3.

FIG. 12.—Longitudinal section through intestinal canal below stomach; *p. e.*, very dense layer of peritoneal epithelium; *st.*, supple layer of supporting lamella; *w.*, wall of intestine; *cil.*, ciliated internal layer of same.

FIG. 13.—Dorso-ventral longitudinal section taken through the median line, showing *p. b. w.*, posterior body-wall with peculiarly modified granular ectodermal cells; *pch.*, semicircular pouch or margin surrounding base of peduncle, *ped.*; *cu.*, thickened cuticle of peduncle; *st.*, network of fine supporting or connective tissue fibres; *p. o. m.*, posterior occlusor muscle. Magn. Oc. iii, Obj. 6.

PLATE XVI.

FIG. 14.—Transverse section from near origin of peduncle from posterior end of ventral valve; *cu.*, the thickened cuticle; *l. bl.*, large blood-vessel; *cp.*, cavity of the semicircular pouch seen in longitudinal section in Fig. 12; *p. b. w.*, modified ectoderm cells of posterior body-wall; *p. o. m.*, diagrammatic representation of attachment of posterior occlusor muscle. Magn. Oc. iii, Obj. 7.

FIG. 15.—Transverse section of portion of mantle, with shell through mantle-sinus showing genital ridge, *g. r.*, filled with

numerous granules of sperm-material; *s. p.*, spermatophores; *h. l.*, horny layers diagrammatically represented; *c. l.*, calcareous layer of shell; *l. c.*, lime-cells; *m. e.*, beginning modification of peritoneal epithelium; *ec.*, general ectodermal covering; *sh.*, shell. Magn. Oc. iii, Obj. 7.

FIG. 16.—Section through mantle in situation of branchial pouch at base of mantle-margin, showing generative ridge and contents; borax-carmin specimen; *ec.*, general ectoderm; *l. c.*, lime-cells; *p. e.*, peritoneal epithelium; *y. o.*, young ova; *sp.*, spermatophores of various sizes, X the point at which peritoneal epithelium begins to become changed. Magn. Oc. ii, Obj. 4.

Fig. 17.—Dorso-ventral longitudinal section through central sub-oesophageal ganglion, showing the ventral half of the ganglion; *ec.*, general ectodermal covering, the cells here running several layers deep; *l. g. c.*, very large multipolar ganglion-cells; *pr.*, peculiar wavy processes emanating from these ganglionic bodies and pursuing an antero-posterior course, finally splitting up into finer branches, and becoming lost in the thick and dense, felty network of fibres bordering on the supporting lamella; *s. t.*, supporting tissue very much thickened. Magn. Oc. iii, Obj. 9.

FIG. 18.—Transverse section through about the centre of the lateral sub-oesophageal ganglion; *ec.*, general ectodermal covering; *l. g. c.*, large multipolar ganglion-cells; *s. t.*, supporting tissue very much thickened in this situation.

FIG. 19.—Section through supra-oesophageal nerve-ganglion and portion of the most anterior extremity of alimentary canal; *g. c.*, probably apolar ganglion-cells imbedded in the wall of the oesophagus; *s. oe. g.*, supra-oesophageal ganglion, in structure essentially the same as the other two, but with smaller cells; separated from the oesophagus by a thick layer of loose supporting tissue, *s. t.*; *ec.*, general ectodermal covering; *p. e.*, peritoneal epithelium of large sub-oesophageal blood-lacune. Borax-carmin spec. Magn. Oc. iii, Obj. 7.

PLATE XVII.

FIG. 20.—Transverse section of anterior extremity of oesophagus and gullet, taken at about the level, marked *v.* in Fig. 6; the drawing is made from the extreme lateral portion of the transverse slit leading into the mouth; *ec.*, general ectodermal covering; *lac.*, blood-lacunes; *a. l.*, extreme lateral portion of anterior lip of mouth; *sp.*, space left between *a. l.*, anterior lip, and *p. l.*, posterior wall of mouth or gullet, and showing cilia; *g. c.*, peculiar large cells with thick and numerous

gr. nules, well-defined and usually eccentric nuclei and nucleoli, probably representing apolar ganglion-cells; *c. c.*, spindle-shaped cells, possessing one or more nuclei and imbedded in *s. t.*, which is to represent the homogeneous supporting substance in this situation; *lac.*, ordinary blood-lacunae. Magnif. Oc. ii, Obj. 9.

FIG. 21.—From a dorso-ventral longitudinal section, showing bands of supporting tissue covered with peritoneal epithelium undergoing modification and in the process of forming ova; *m. p.*, modified peritoneal epithelium; *f. d. o.*, fully developed ova, ready to drop off, always to be found at the most dependent portion of these genital bands suspended from the oviducts and mesenteric bands. Picrocarmine specimen. Magn. Oc. iii, Obj. 9.



Fig 1.



Fig 2.

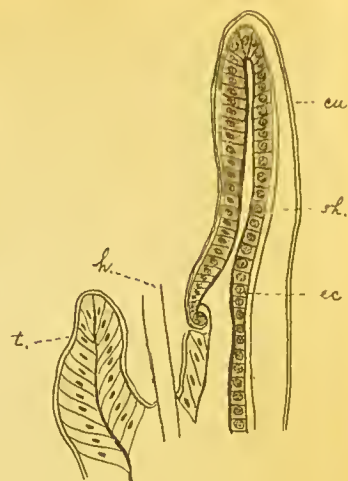


Fig 3.



Fig 4.

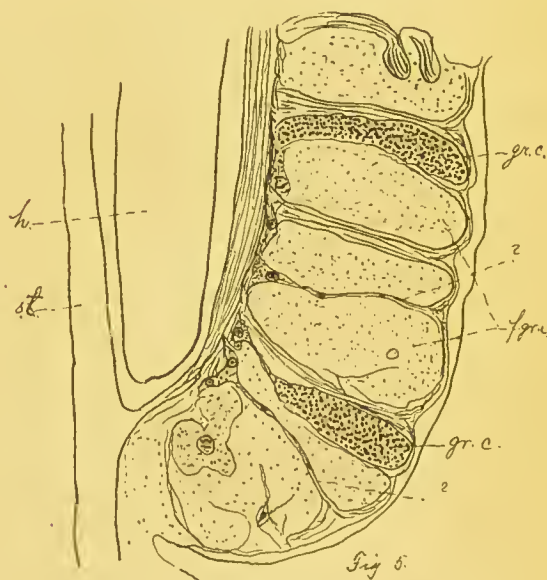
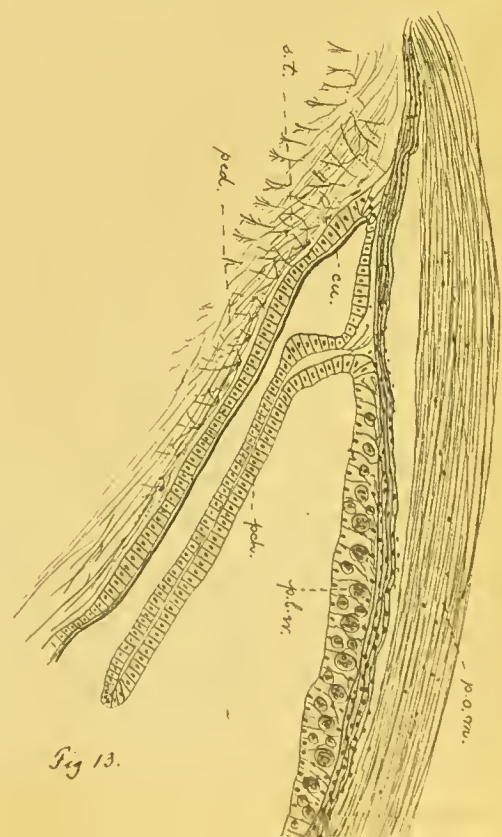
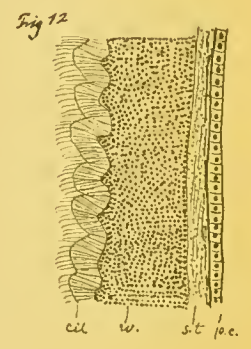
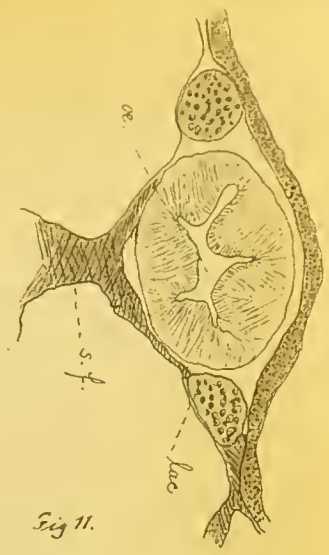
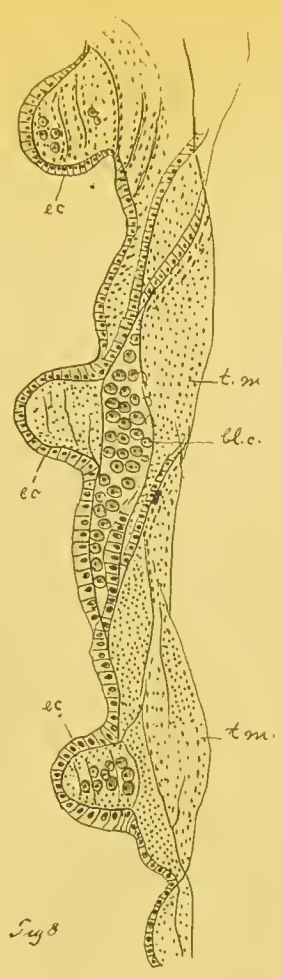
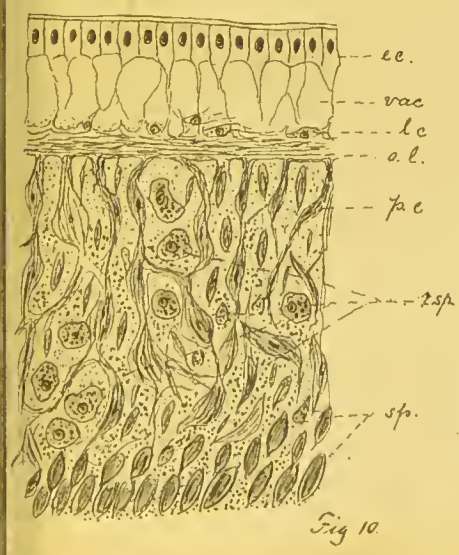
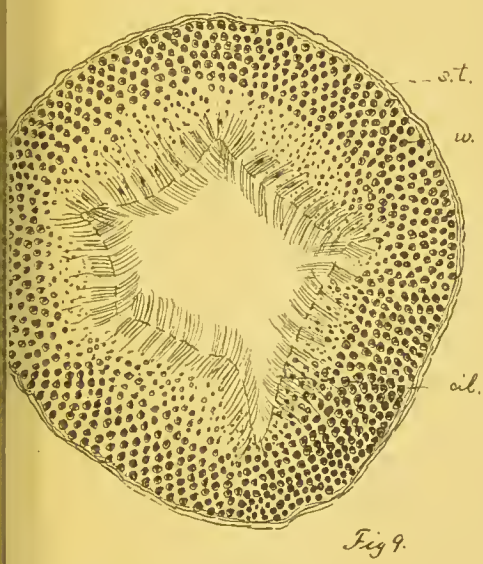
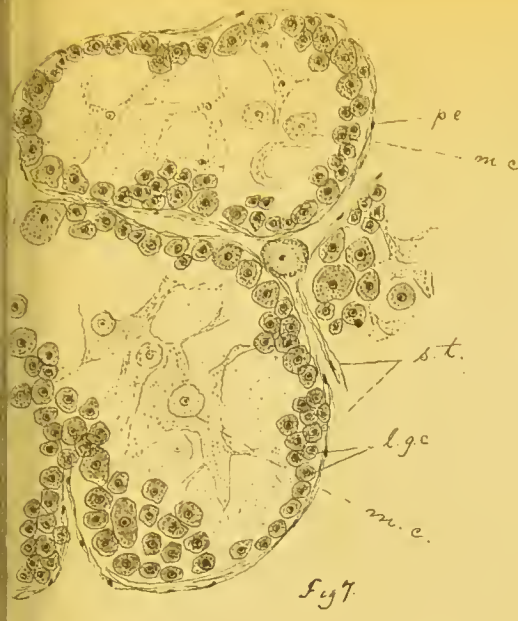


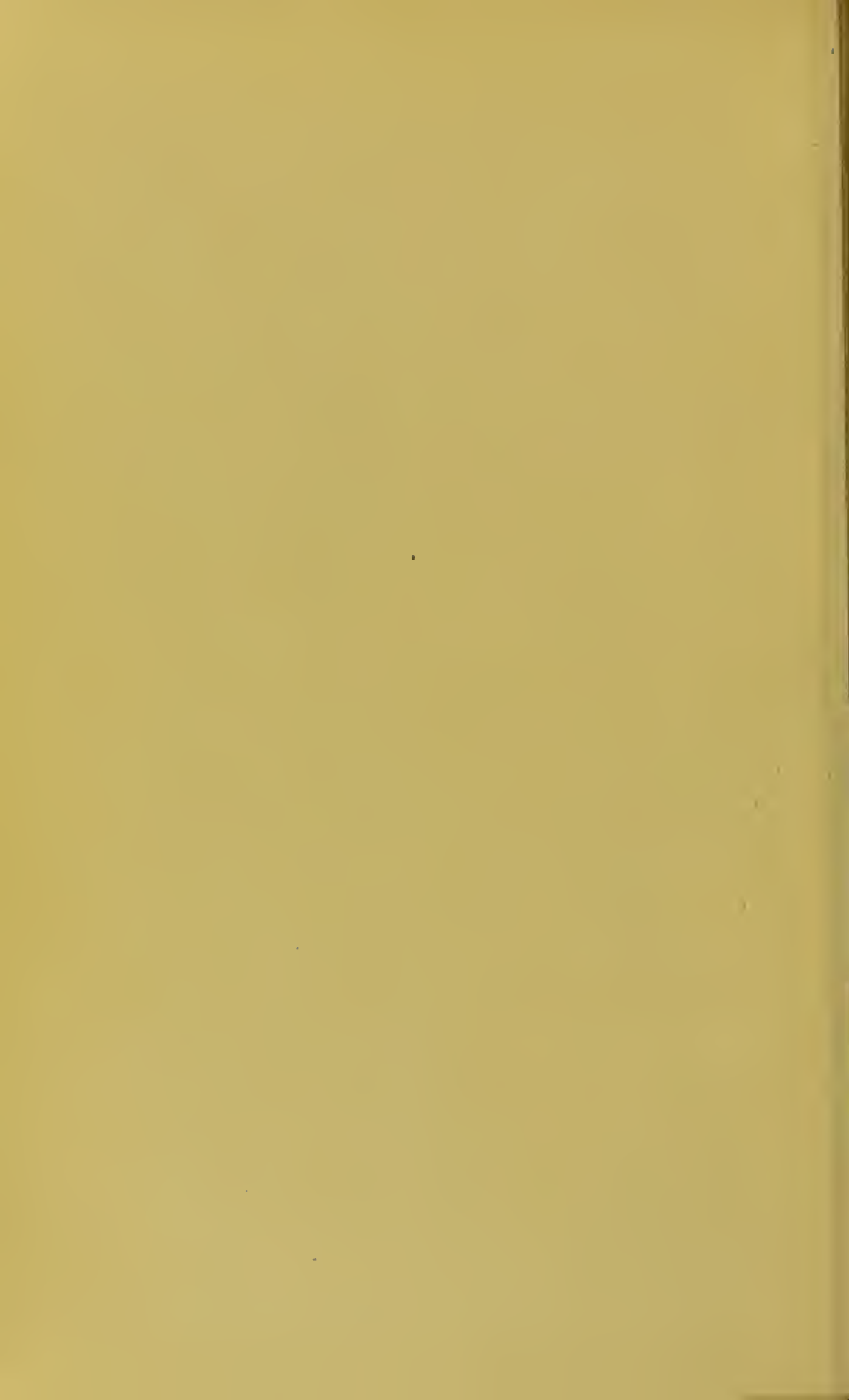
Fig 5.



n. 5.







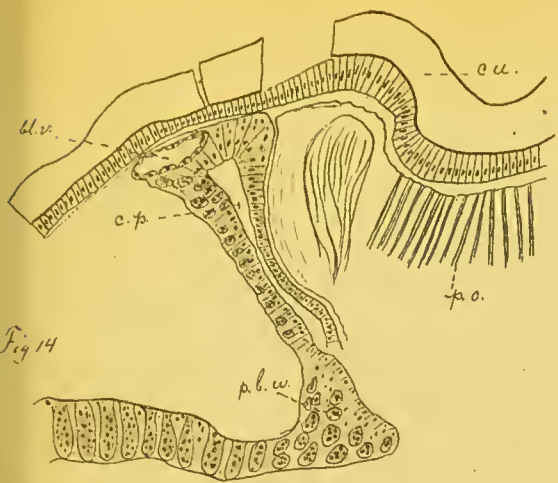


Fig 14

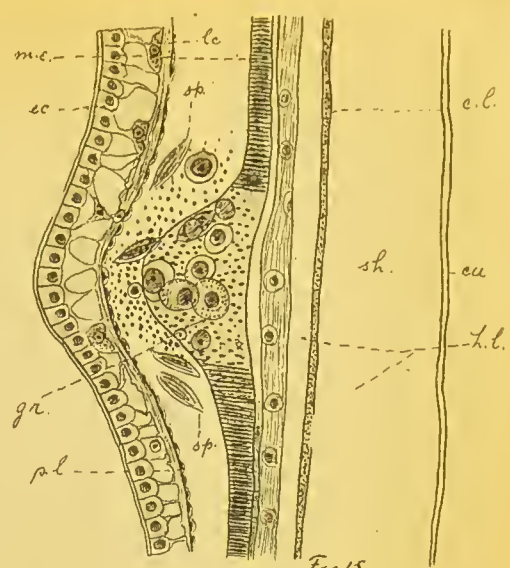


Fig 15

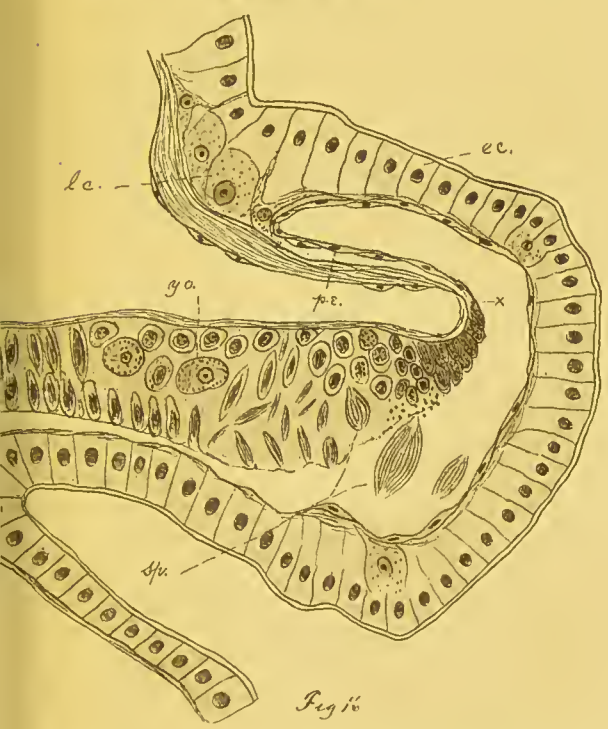


Fig 16

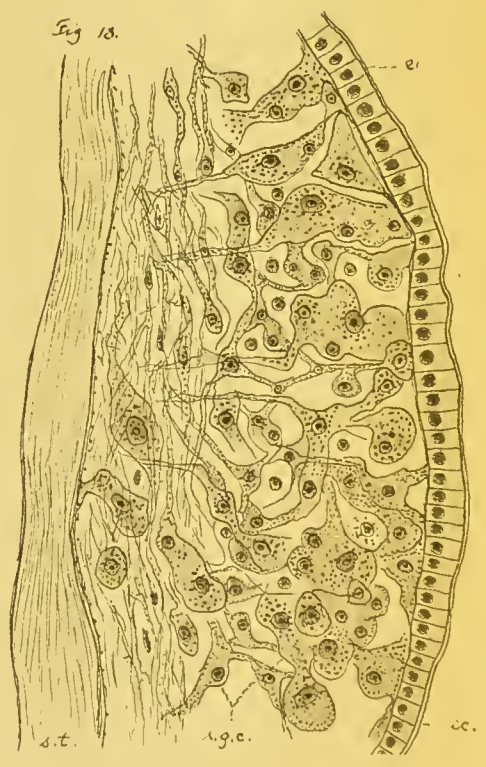


Fig 18

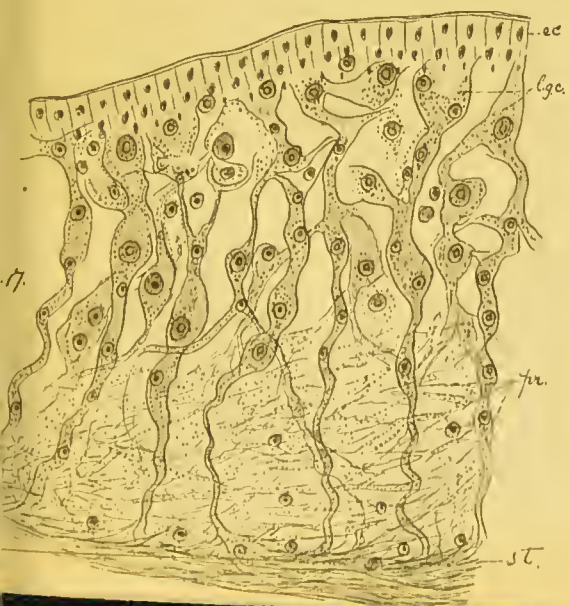


Fig 17

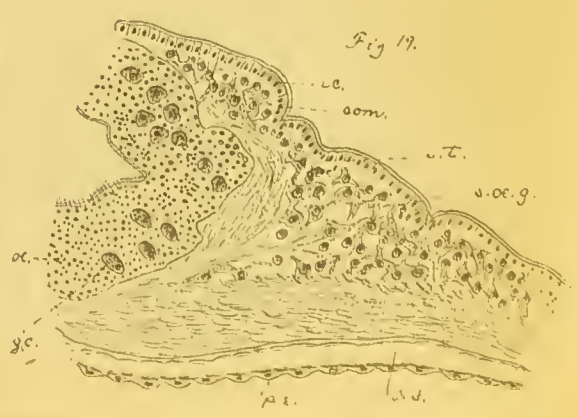


Fig 19



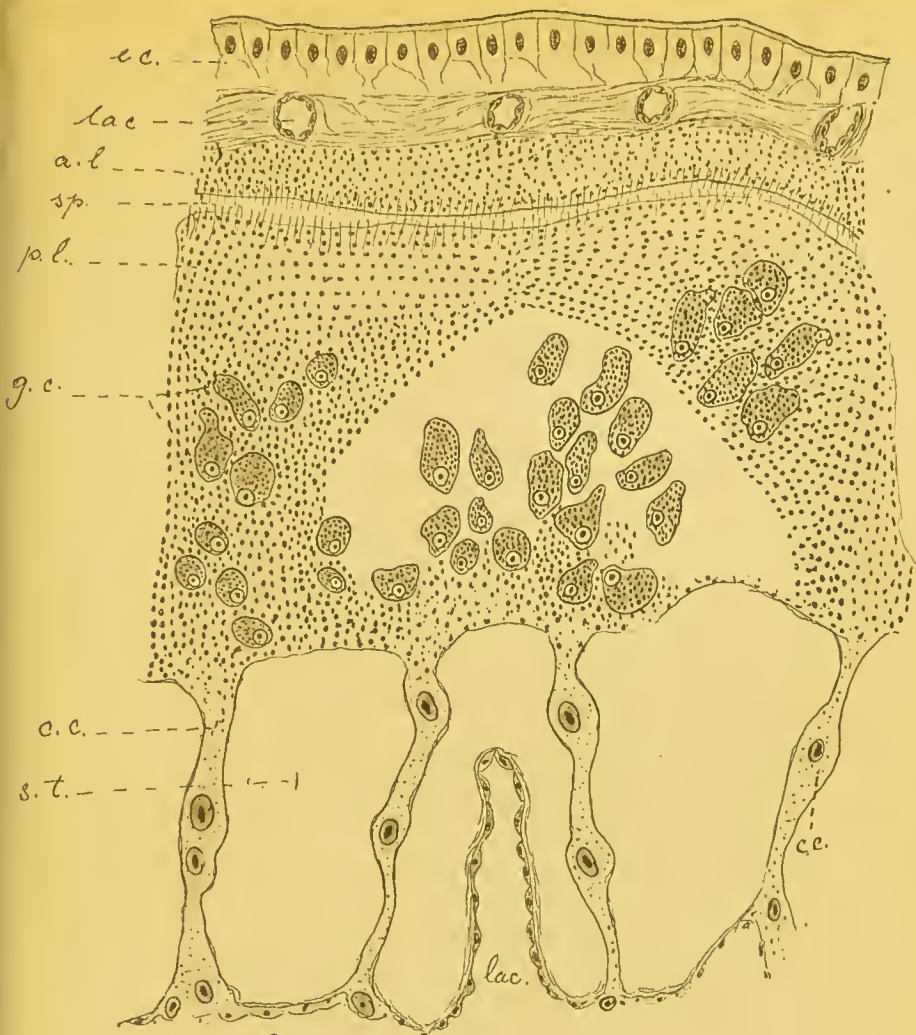


Fig 20



